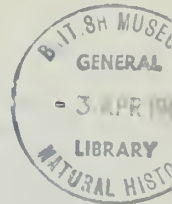


The Yorkshire Jurassic fern *Phlebopteris braunii* (Goeppert) and its reference to *Matonia* R. Br.



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Synopsis

Recently-collected material of the matoniaceous fern *Phlebopteris braunii* (Goeppert), first described and best known from the Lower Lias of Germany, is described from the Middle Jurassic (Bajocian) of Yorkshire. The Yorkshire leaves are shown to have indusiate sori like the living *Matonia pectinata* R. Br., whereas the Liassic *P. braunii* was firmly believed to have naked sori. Search has however revealed an indusium in Liassic specimens also, and reasons why it had been missed are suggested. *Phlebopteris muensteri* (Schenk 1867) is regarded as a synonym of *P. braunii* and the combined species is renamed *Matonia braunii* (Goeppert) n. comb.

The present status of the Yorkshire Jurassic Matoniaceae is considered. A few specimens of *M. braunii* had been mistakenly identified with other species, blurring their definition. In addition, reasons are given for conserving the specific name *braunii* Goeppert 1841 against names of certain Yorkshire specimens described earlier. The early descriptions of fossil Matoniaceae are also reviewed in general, with notes on the type status of some of the specimens.

Introduction

Fronds agreeing with the well-known Lower Liassic fern *Phlebopteris braunii* (Goeppert) (*P. muensteri* (Schenk)) were collected from the Bajocian of Yorkshire in 1972–73. When suitably prepared the new specimens proved to have indusiate sori like the living *Matonia* whereas *P. braunii* was believed to have naked sori, a position which seemed, at first, confusing. I then realized that certain Yorkshire specimens which I had identified with *Matonidium goeppertii*

Schenk because they possessed indusia agreed better with the new material. Later still I found that specimens collected from the classic Gristhorpe Bed and described early in the nineteenth century under various names were also similar; see notes on p. 301. Finally I found that *Phlebopteris braunii* itself, from the original localities in the Lias of Bavaria and from East Greenland, also has indusiate sori.

When exposed by splitting the rock, most of the new fronds show their upper surface, and the fertile pinnules only reveal their sori satisfactorily when prepared as transfers. However, a number of Lower Liassic specimens from Bavaria and from Greenland show their lower surface as collected, and since their indusia are in most cases missing the sporangia are seen clearly. There thus seemed no point to early workers, including myself, in preparing transfers of such specimens. Certain Greenland specimens did show sori covered by indusia but when I worked on them 50 years ago I dismissed them as unsatisfactory and kept them merely as duplicates for exchange. Apparently Bavarian collectors did the same. Happily the duplicates were sent to the British Museum (Natural History) and I re-examined them recently, when ready to perceive their nature.

Harris (1931) gave reasons for identifying *Phlebopteris muensteri* (Schenk) with *P. braunii* (Goepfert), a conclusion to which I adhere. The discovery of the indusium, however, distinguishes the combined species from the genus *Phlebopteris*, and it is here placed in *Matonia*, as *Matonia braunii* (Goepfert) n. comb.

Material

Most of the new specimens were collected from the Hillhouse Nab Plant Bed, Farndale, at about 54°23'3''N, 0°59'0''W. This bed was first found in about 1950 and consists of a 2 m thick and rather extensive layer of plant-bearing rocks at the base of the deltaic beds. Like many other Yorkshire plant beds it includes lenticles providing abundant specimens of a particular species and one such lenticle, about 2 m broad and 10 cm thick, gave the specimens described here. This lenticle is the only rich source of *P. braunii* in Yorkshire though material had earlier been collected at Saltwick, also at the base of the deltaics, and from the Gristhorpe Bed at a higher level, but only as occasional specimens.

The Hillhouse Nab matrix is a fragile silty shale and rarely gave blocks more than 20 cm wide. Together with overlap of the crowded fronds this limited the size of the specimens as collected, though some of the fronds may well have been complete when deposited. The matrix is one in which the coaly substance of fern and other leaves with delicate cuticles has become crossed by fine cracks and is apt to crumble away as dust. This is the cause of gaps in drawings of the veins (Figs 5, 6, 15). In most leaves the lamina is opaque but in some layers it had undergone oxidative decay at or following deposition, and the veins show as dark strands on a brown lamina. Otherwise the lateral veins, if seen at all, are marked only by their elongated epidermal cells though the midribs form a small ridge above and a larger ridge below. Most fertile pinnules merely show their sori as obscure bulges on the upper surface and when transferred prove denuded, showing the placenta as a boss. But the best leaves have sori which retain both their sporangia and indusia (though these are apt to be damaged when a transfer is made). Nearly all sporangia were found to be empty when macerated but one was full of ripe spores.

The Gristhorpe and Saltwick specimens are as well preserved as Lower Lias ones and compared with the Hillhouse Nab material the lamina is less completely flattened and the coaly substance more coherent.

Description

Frond form. All the new specimens are somewhat damaged and not one shows a perfect frond centre spread out in a symmetrical fan as in a carefully pressed leaf of *Matonia pectinata*. The specimen in Fig. 1 is the left half of a frond centre, together with a small, probably extraneous axis on the right. The pinna rachises increase in width, left to right, from 1.2 to 1.6 mm and they are borne at the end of a bare 'arm'. Some herbarium specimens of *M. pectinata* in the



Figs 1–6 *Matonia braunii* (Goepfert) comb. nov. Hillhouse Nab, Farndale. Fig. 1. Half of leaf centre, drawn from part and counterpart, V.59743, $\times 1$. The separate axis on right is probably extraneous. Fig. 2. Half of leaf centre, drawn from part and counterpart, V.59744, $\times 1$. Top of rachis twisted and folded. Fig. 3. Apex of fertile pinna, V.59748, $\times 1$. Fig. 4. Apex of sterile pinna, V.59744, $\times 1$. Fig. 5. Venation of small sterile pinnule, shown on imprint of under surface, V.59746, $\times 6$. Vein meshes are numerous in this specimen. Fig. 6. Venation of lowest pinnule from pinna in Fig. 8, p. 298. At \times note the branch vein which ends blindly at a point where a placenta might be expected. V.59745, $\times 5$.

BM(NH) show 'arms' bare below and could provide such a fragment. The frond centre in Fig. 2 shows the right half only; the left 'arm' may be folded beneath or missing and the rachis has been folded in compression. Eleven pinnae have rachises about 1.0 mm wide but the two on the right are narrower. None of the specimens contributes to settling the controversial architecture of the frond centre discussed by Hirmer (1927), Hirmer & Hoerhammer (1936), Lundblad (1950) and Appert (1973) as well as others cited by them.

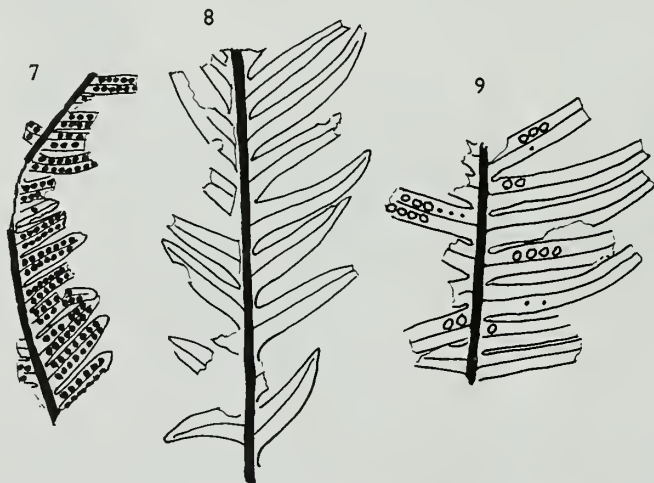
No Hillhouse block gives the full length of a pinna, though from the taper of the rachis I estimate it about 20 cm long. The pinna rachis grades into a wing of lamina, making it hard to measure its width accurately. Over most of a pinna the pinnules remain uniform but at the base they become shorter and broader and finally merge as a continuous wing (Fig. 1). At the apex they become narrower and are borne at a smaller angle, and if fertile they have few sori (Fig. 3). If sterile they look like a *Cladophlebis* with very oblique veins (Fig. 4).

At Hillhouse Nab, where no large leaves are known, the larger pinnae have pinnules 18–25 mm

× 3.5 mm, the smaller pinnae having pinnules 11×2.5 mm. In the Gristhorpe Bed pinnules larger than Hillhouse ones occur, along with small ones.

Adjacent pinnules of all specimens are connected by a web of lamina 0.5–1.0 mm wide though this web has often suffered in preservation. The pinnule margins are in contact in some fronds but separated by gaps up to 3 mm wide in others. In fertile fronds and most sterile ones the pinnule margins of the longer pinnules (Figs 7, 9) are parallel to near the apex but in a few sterile fronds the pinnules taper from a broad base (Figs 6, 8); this is the typical '*braunii*' form as distinct from the '*muensteri*' form. Intermediate forms are frequent. The classic Bavarian material named *Laccopteris braunii* (Goeppert 1841) included a remarkable series of small leaves, *L. germinans*, which are generally accepted as belonging to juvenile plants, but the Yorkshire collections include no such specimen.

Sterile Hillhouse pinnules are flat, apart from the raised midrib. In transfers their margins are dark and possibly fibrous. The fertile pinnules are nearly flat but the margins may be slightly depressed. Above each sorus there is a bulge, broad in some pinnae, small in others and never very pronounced. It may be so low that the presence of a sorus is uncertain until a transfer is made. In the Gristhorpe matrix the sterile lamina is slightly convex between midrib and margins and more strongly convex in fertile ones.



Figs 7–9 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. All × 1. Fig. 7. Pinna with short, densely fertile pinnules, V.59746. Fig. 8. Sterile pinna with broad-based pinnules, venation shown in Fig. 6, p. 297. Part, V.59745. Fig. 9. Pinna with longer and sparsely fertile pinnules, V.59747.

Venation. In sterile pinnules and in sterile parts of fertile pinnules the veins characteristically fork twice and their branches run obliquely, meeting the margin at 35° . Very occasional veins of large pinnules anastomose, the union being near the midrib or further out and thus irregular (Fig. 5). Many pinnules and all the smaller ones have no anastomosis at all. In the smallest pinnules and in the apical parts of large ones the veins fork only once. In the basal flange along the rachis there is a forward-running branch vein which joins a backward one from the next pinnule, and from the combined vein further branches run to the sinus, though often this part is poorly preserved. All vein branches end in the margin.

In fertile regions of the pinnules each lateral vein has a forward branch ending at the sorus and an outward branch which forks, the branchlet nearest the rachis meeting the margin nearly at a right angle (Fig. 18, p. 302). There are no anastomoses except in the basal web between pinnules.

No vein or rachis shows any hairs or scales, either directly or in transfer.

Sori. Although the upper surface of the lamina is the one exposed in all the Yorkshire specimens, the coaly substance has sometimes crumbled away to reveal sporangia, though I did not recognize

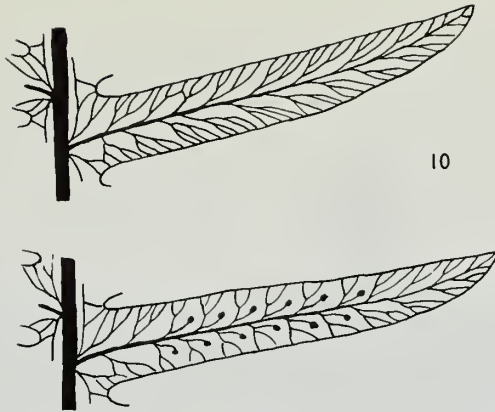
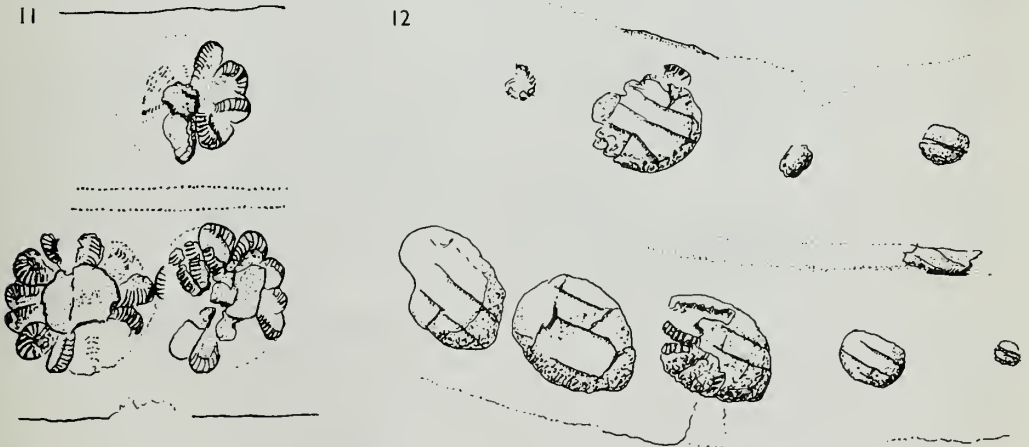


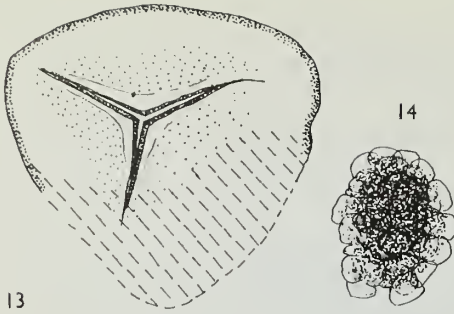
Fig. 10 Diagrams comparing the venation of sterile and partly fertile pinnules of *Matonia braunii*. Note that both are often relatively longer. A higher proportion of sterile veins may anastomose. Fertile pinnules are often more fully fertile, relatively narrower and have narrower webs along the rachis.

the indusium. In transfers of the more perfect fertile specimens the state of the sori varies, even between adjacent sori. In its most perfect state, however, the sorus is entirely covered by the large convex indusium (Fig. 12). Often this is partly broken in preparation and then the outer parts of sporangia are visible; sometimes only the middle of the indusium remains (Fig. 11). More often both indusium and sporangia have been lost, apparently before the preparation was made, and nothing remains but the projecting placenta (Harris 1961: fig. 38D, named *Matonidium*); I consider that this loss occurred before preparation because I believe I can distinguish between the bright surface of coal fractured in preparation and the dull surface of coal preserved in contact with mud. Not one Hillhouse specimen showed a sorus of ripe but undischarged sporangia exposed by the loss of the indusium, though sori in this state have been figured from Bavaria and from Greenland.

Many Hillhouse sporangia were macerated and proved empty but one from an otherwise empty sorus gave a coherent mass of spores (Fig. 14). The maceration failed to separate them but I



Figs 11–12 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. Transfers of fertile pinnules, $\times 20$. Fig. 11. V. 59750. The sori have crumbled in preparation, the upper one having lost its indusium and the lower ones all but some of the middle portion. Fig. 12. V.59751. The indusia are intact apart from cracks caused by shrinking. The small sori to the right are abortive and at the top left there is a denuded placenta.

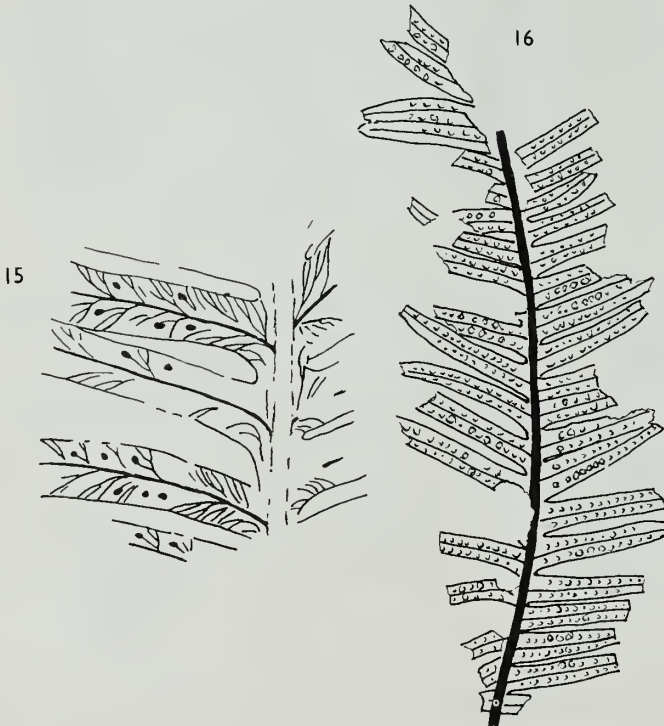


Figs 13–14 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. V.59752a. Fig. 13. Spore at the edge of the mass shown in Fig. 14, $\times 800$. The shaded part is obscured by overlapping spores. Fig. 14. Spore mass isolated from a sporangium *in situ*, $\times 80$. Some of the spores are outlined more definitely than is certain.

estimate their number at about 100. The spores have smooth brown walls about $1.5\ \mu\text{m}$ thick and the one most clearly seen (Fig. 13) is figured. They are about $50\ \mu\text{m}$ wide. As the spores are coherent and smooth-walled it is possible that they died before maturing and the fact that this was the only sporangium of the sorus which yielded spores also implies arrested development. Harris (1961) figured a similar spore from a Gristhorpe specimen and a smaller one from a Saltwick specimen, both as *Matonidium*.

Discussion

The indusium. I determined the new specimens in the field as *Phlebopteris braunii* because they agreed in every character visible with a lens. But when I made transfers and found that the sori



Figs 15–16 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. Fig. 15. Partly fertile pinna in transfer, V.59749, $\times 3$. The placenta are small and possibly abortive. Fig. 16. Longest available pinna fragment, sori obscure. V.59748, $\times 1$.

had indusia I decided this was impossible. Like others I was convinced that *P. braunii* had naked sori, this being the character that distinguishes *Phlebopteris* from *Matonia*. There seemed a grave practical difficulty. There were two groups of well-preserved specimens, *P. braunii* in the Lower Lias of western Europe and East Greenland in which certain specimens, though a minority, showed naked sori, and the new Yorkshire group in which certain specimens showed indusia when transferred. But most specimens were indistinguishable and this applied also to nearly all those figured previously except the ones showing details of sori. It seemed that the groups were generically distinct but could seldom be distinguished and I tried to escape from the difficulty with elaborate hypotheses.

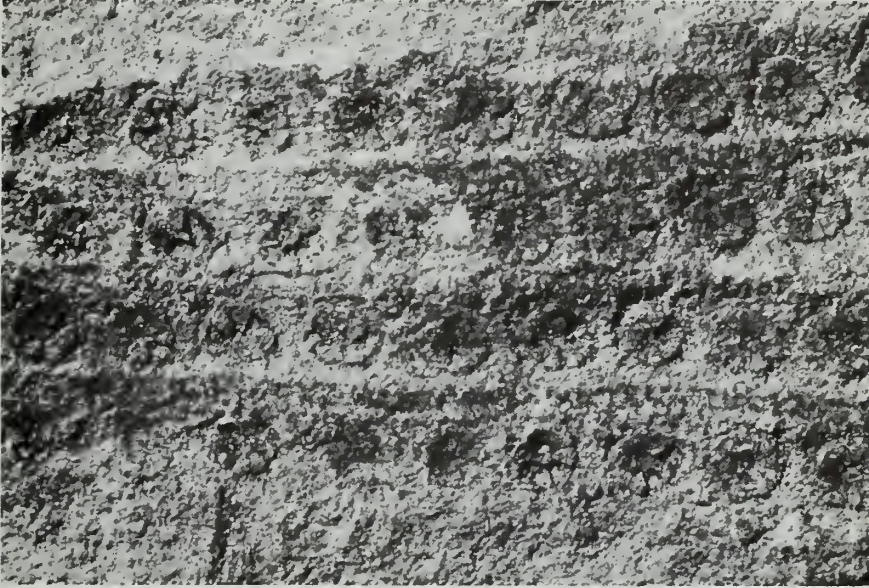


Fig. 17 Two pinnules of *Matonia braunii*, V.21660, Scoresby Sound, East Greenland, $\times 10$. Shrinkage after collection caused cracks to form in the indusium between the sporangia and around the placenta. The sporangia contain ripe spores but their annulus is not visible.

Later, when I saw Liassic specimens of *P. braunii* in the BM(NH) the difficulty vanished. *P. braunii* also has an indusium but is apt to lose it. I suggest that collectors selected against specimens with sori concealed by indusia, as I evidently did in Greenland.

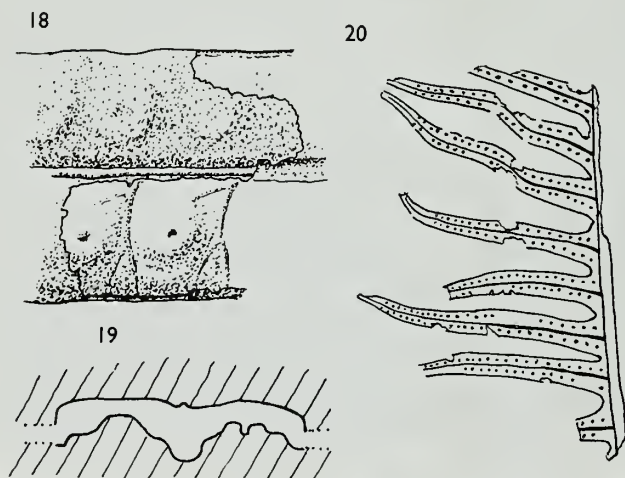
For example, specimen 15043 from Bayreuth, Bavaria, labelled *Lacopteris muensteri*, shows the under-surface of many fertile pinnules, some with intact sori, others denuded. In the intact sori the sporangia form vague bulges but do not show their annulus cells and I conclude that this is because they are covered by an indusium. The evidence is not fully convincing because it is possible that this specimen had been coated with varnish which obliterated them, although I see no sign of any such varnish.

Equally, specimen V.21660, collected by me from the Lower Lias of East Greenland and sent by the Copenhagen Museum in exchange, has sori with an essentially smooth surface though the coaly substance has shrunk since being collected and there is a circular crack around the placenta. There are radial cracks between sporangia but nothing at all of their annulus cells is to be seen (Fig. 17).

There is thus no difference between the indusiate sori of the Yorkshire specimens and the Lower Liassic ones. There is, however, a difference in size between the Yorkshire and the Liassic leaves, recognizable in the pinnules. Those from Hillhouse Nab range from about 12 mm to 25 mm in length and one pinna from the Gristhorpe bed has pinnules 35 mm long. Mature and fertile Liassic leaves also range from about 12 mm upwards, but many specimens are 50 mm or more

long; the largest seen (Bavarian) was almost 100 mm \times 5 mm. As I can find no other difference I suppose that the Yorkshire environment, particularly at Hillhouse Nab, was unfavourable to the production of very large leaves. The fact that scarcely any unopened sporangia are preserved there suggests that the air may have been dry.

Contour of fertile pinnule. Hirmer & Hoerhammer (1936) illustrated the variation in the surface contour of the fertile pinnule (in specimens named *P. muensteri*), and similar variation has been seen in the Greenland and Yorkshire material. Their pl. 3, figs 3, 3a show a nearly flat upper surface and their pl. 5, fig. 1 a nearly flat lower surface. On the other hand their pl. 3, fig. 6, of the upper surface of another pinnule, shows high mounds above the sori and depressions near the midrib and margins. Their pl. 4, fig. 6 of the under surface is the reverse; the midrib and margins are strongly raised and they are connected by transverse ridges which mark out hollows where the sori were situated. No Yorkshire specimen is as strongly contoured as this, though some approach it.



Figs 18–20 *Matonia braunii* (Goeppert) comb. nov. Gristhorpe Bed, V.31982. Fig. 18. Part of a pinnule of Fig. 20, \times 10. The imprint is seen below and to the right, the coaly substance of the lamina above and to the left. Fig. 19. Diagrams representing the contour of the imprints of the pinna of Figs 18 and 20 and an inverted pinna on the same block. Horizontal scale of lower section \times 10, of upper \times 13, vertical scale increased four times to compensate for matrix compression. Fig. 20. Pinna \times 1. The sori are shown as dots representing the placenta, but some in addition show the indusium or the sporangia. A transfer of the counterpart, V.31982a, was figured by Harris (1961: figs 38A–D) as *Matonidium*.

The absolute difference in elevation differs in different matrices; in the Yorkshire specimens it is lower for example in the Hillhouse siltstone than in the Gristhorpe claystone but in each the range is of the same kind. The differences can be explained on Walton's (1936) theory of the changes which occur when a plant organ is compressed in a less compressible matrix, the final form being determined by the surface which originally faced downwards. The original shape of a fertile *M. braunii* pinnule can thus be deduced from the shape of its upper and lower surfaces. Original differences in different pinnules may have occurred also, though it is unnecessary to invoke them to explain what is seen in the fossils.

Specimen V.31982 from Gristhorpe is helpful in working out pinnule contour because it shows three pinnae, two in normal orientation and one inverted, and in all three some of the coal remains but most is missing and the imprint is exposed. By comparison with other blocks I infer that this specimen has the same orientation as when it was part of the Gristhorpe Bed. The imprints and remaining coal are illustrated (Figs 18–20) as seen under very oblique lighting. In describing the imprints I reverse the words 'high' and 'low' as though describing the fossil that made the imprint.

The upper surface (shown by the imprint of the inverted pinnules, Fig. 20 and upper part of 19) has low relief, high regions being at most 100 μm above low ones. The midrib forms a narrow ridge bounded by shallow grooves in the lamina and the margins are depressed. The sori form scarcely perceptible bulges. The lateral veins are sometimes visible as very low ridges. Leaf substance remaining as coal, the original under surface, has just the same relief though the midrib is broader and the placenta and occasionally indusia can be seen (but are nearly flat).

The imprint of the lower surface (shown by the normally orientated pinnules, Fig. 18 and lower part of 19) has relief of up to 200 μm . The broad midrib and the margins are prominent and the sori form conspicuous hollows usually with a central boss, the placenta, sometimes still with the indusium or part of it. One sorus shows the imprint of a full set of sporangia but no indusium. Again the upper surface is mainly just the same but the midrib is narrow and the strong soral bulges often have a dimple above the placenta. The lateral veins may be fairly conspicuous as ridges on the lower surface but the branch to the sorus is usually concealed in the soral pit.

Walton's (1936) theory includes the effects of compression of the matrix. This causes a general and proportionate lowering of relief. Certain pinnules are distorted and tilted, and from their apparent narrowing and the elevation of the raised side I estimate that this sample of the Gristhorpe clay was compressed to about one quarter. I use this figure in reconstructing the original shape of the pinnule (Fig. 19), but unfortunately no laterally compressed pinnule is available to show its original thickness. I have merely made the lamina thick enough to allow for the difference between the deep soral pit below and the low mound above.

The matrix of V.31982 is too coarse to show the imprint of epidermal cells like those illustrated by Appert (1973). He comments (1973: 28) on the difference between his figure of collodion imprints and the figures of Schenk (1867) which apparently represent macerated cuticles. My own efforts to prepare a cuticle from Greenland and from Yorkshire ferns failed. I suggest that Schenk figured a fragment of gymnosperm cuticle which adhered to his specimen.

Identity of *Phlebopteris muensteri* with *P. braunii*. It is convenient to consider this aspect of the taxonomy before identifying the Yorkshire specimens with both. Hirmer (1927) united the two taxa under *Laccopteris elegans* Presl, a species he later placed—with no good reason—in the Marattiales. Hirmer & Hoerhammer (1936), however, separated them and set out the differences in detail. They have been followed in this by most authors, though Kräusel (1958) expressed doubt. On the other hand some have firmly united them under *Phlebopteris muensteri* Schenk, chiefly Harris (1931), Reymanówna (1963), Weber (1968) and Appert (1973). (Goepfert's name *braunii* has priority and possibly these authors mistakenly used *muensteri* because Schenk's fertile specimens were better).

The evidence for identity is simple; the two forms occur together in the field and they intergrade morphologically. Thus they are recorded from the same localities in Bavaria (though I know no details). In Greenland the material was only locally common but was found in five localities and in each the two forms are closely associated (Harris 1931). The two forms also occur together in Yorkshire, particularly at Hillhouse Nab and in the Gristhorpe Bed.

Leaves of the *braunii* form have in fact the appearance of shade leaves. They are always sterile and have a broad, flat lamina showing the veins very clearly. Their pinnules may be triangular and always taper from the base. Leaves of the typical *muensteri* form on the other hand may be sterile or fertile. Their pinnae are long, relatively narrow and parallel-sided to near the apex. The substance of the lamina is thick and the veins are hard to see until a transfer is prepared, when the branching of the lateral veins is seen to be of *braunii* form in sterile pinnules but different in fertile ones. The pinnule margins are often bent downwards in fertile leaves.

Hirmer & Hoerhammer stated additional differences regarded by them as of specific rank but they do not even apply to all the specimens they themselves figured. The most impressive evidence of identity of the two forms is probably from partly fertile specimens, where *braunii* venation is seen in the sterile portions but *muensteri* where there are sori; see for example Harris (1926: text-fig. 6 A, E as '*Laccopteris groenlandica*'; 1961: fig. 37E as *Matonidium goepfertii*) and Fig. 15, p. 300 here.

Identification of Yorkshire specimens. There is no doubt that all the Hillhouse Nab specimens belong to a single species. They are numerous and intergrade, the mean is the most frequent form and the more complete specimens show much of the range of form in the one frond. No similar species is associated with them.

The Gristhorpe Bed specimens are few, though even there a number of fragments may occur on one block. A difficulty is that *Phlebopteris polypodioides* also occurs there and is more frequent, but it is usually easy to distinguish. The specimens accepted as *M. braunii* are like those from Hillhouse Nab but are better preserved and some are larger; one pinna has pinnules 35 mm × 3.5 mm (the largest at Hillhouse Nab was 25 mm × 3.5 mm); if Lindley & Hutton's figure (1831–33: pl. 60) accurately represents *M. braunii* they may be at least 5 mm wide.

At Saltwick a few fragments only were obtained, from a place where it was difficult to collect.

As all of these Yorkshire specimens agree in fine details I identify them with one another confidently.

Reference of *Phlebopteris braunii* to *Matonia*. The genera of Mesozoic Matoniaceae were formerly distinguished on vague and undefined characters, for instance *Matonidium* Schenk on its resemblance in aspect to *Matonia pectinata*. We owe clear distinctions to Hirmer & Hoerhammer (1936). The genera dealt with here differ in a single organ, the indusium. *Phlebopteris* had no indusium at all, *Matonidium* had a placenta which expanded slightly and covered the bases of the sporangia and living *Matonia* has the sorus entirely covered by the indusium. Since *P. braunii* has a large indusium it must be removed from *Phlebopteris* and does not fit *Matonidium*, so the only question is whether it should be placed in the living genus *Matonia*.

Only late in this study did I realize that *Matonia pectinata*, like *P. braunii*, may also show naked sori through loss of the indusium. Seward (1899) figured such a sorus in detail whilst a photograph in Hirmer & Hoerhammer (1936: text-fig. A) shows a herbarium specimen with some sori indusiate and others naked.

I have examined herbarium specimens of *M. pectinata* in the BM (NH) and other herbaria. Fronds with small sori which I presume are immature retain all their indusia but those with full-sized sori nearly all show some sporangia exposed by the loss of the indusium. There is nothing to show whether the indusium dropped off while the frond was alive, as apparently happened in the specimen figured by Seward (1899), or only after it had been dried for the herbarium. But no frond shows all its sori exposed as do certain Lower Liassic ones of *M. braunii*. The excellent Liassic specimens of *M. braunii* showing all their sporangia exposed but still full of ripe spores must be counted as biological failures since they died without releasing their spores, a fate which happens to modern ferns living in continuously damp air. In this respect the Middle Jurassic Hillhouse Nab specimens are more normal since almost every sorus has discharged all its spores.

I can find no account of the behaviour of *Matonia* sori as they ripen. However, I fortunately consulted Mr A. C. Jermy (Department of Botany, BM (NH)) shortly before his recent visit to Sarawak and he gave me the following interesting information about *Matonia* by letter.

I was able to find it on the mountain ridges of Gunong Mulu. It was growing at about a 5000 ft [1500 m] altitude in those areas which had been bared by land-slips and also partly in glades in the *Lithospermum-Quercus* woodland growing on the crest of the ridges. I looked at many fronds to see if the indusium was falling to expose the sporangium, but in no case did I find this was so. For the most part I should add that the complete sorus was attached, although on many fronds the slightest touch would remove them *in toto*, leaving the characteristic papilla-like receptacle.

I then collected a number of mature fronds and exposed them to the sun. I found that the indusium on these shrivelled or partially folded back thus exposing the very short-stalked sporangia which very soon dehisced.

I also found *Phanerorosus sarmentosus* on this trip. This is a fascinating fern, hanging in festoons against limestone cliffs, with fronds up to 20 ft [6 m] or more. It behaved in the same way as *Matonia* except here there were occasional sori which *had* lost their indusia.

The sori of the leaves described must have been fully ripe, riper than on most of the herbarium fronds I have seen. There is thus a difference of behaviour between our fossil and the living Matoniaceae, but perhaps a slight approach in *Phanerorosus*. Clearly in *M. braunii*, under some

conditions in the Liassic at least, the ripe sori may have lost all their indusia before any sporangia dehisced. The fronds were lost from the plant, transported by water and buried with intact sporangia but I cannot tell what interval there may have been between loss of the indusia and of the fronds. I can only imagine that continuous damp weather led to the failure of the sporangia to dehisce, but clearly the difference between *M. pectinata* and *M. braunii* is real. This occurrence of intact sporangia in the fossil Matoniaceae of the Lias is not unique, for in the Yorkshire Oolite many leaves of *Todites williamsonii* and *Klukia exilis* have all their sporangia intact, but containing apparently ripe spores.

M. braunii has much larger pinnules than *M. pectinata* and different venation; in particular its sorus is supplied by a single vein, not several. However, similar differences have been accepted in the fossil genus *Phlebopteris* (the sorus of *P. dunkeri* being supplied just as in *M. pectinata*) and I treat these differences between the living and fossil *Matonia* species as specific rather than generic. It is hard to assess the importance to attach to the different behaviour of the indusia of *M. braunii*, which is partly demonstrable but partly hypothesis, but again I treat it as less than generic. There is a major difference in habitat for it is impossible that fronds should be transported from mountain tops to deltaic pools and buried intact or as large pieces in considerable numbers. Clearly the present observations on the indusium of *M. braunii* call for fresh study of the sori of other fossil Matoniaceae. This study would be best made by transfer preparations of fronds with slightly immature sori facing downwards into the rock. No such study has been made but since in *P. polypodioides* the exposed sorus shows nothing suggesting a central scar, I think there was probably no indusium in this species.

I designate the species as *Matonia braunii* (Goeppert) n. comb. As lectotype I designate the specimen named *Lacopteris braunii* by Goeppert (1841: pl. 5, fig. 1), refigured by Schenk (1867: pl. 23, fig. 12) and by Hirmer & Hoerhammer (1936: pl. 2, fig. 1).

Matonia mesozoica Appert 1973, based on abundant, well-preserved material from the Upper Jurassic of Madagascar, is distinguished from *M. braunii* by its short, broad-based and triangular pinnules up to 9 mm × 3 mm. The sterile veins branch twice as in *M. braunii*. Anastomoses, apart from one in the basal web, are rare.

Comparison of *M. braunii* with Yorkshire Matoniaceae. The recognition of *Matonia braunii* called for reassessment of the Yorkshire Matoniaceae in general, and in particular those with indusia, which had been referred to *Matonidium* on this one character. There are changes in three species but these are slight and most of the specimens remain undisturbed: the species are *Matonidium goepperti*, *Phlebopteris woodwardii* and *P. polypodioides*.

The following comparison consists of short statements of the main diagnostic characters of these three species, drawn up as far as possible in the same manner, preceded by a statement of *M. braunii*.

Matonia braunii (Goeppert, 1841), Yorkshire material. Pinnules 12–35 mm × 2.5–3.5 mm, rarely 5 mm, basal connecting web up to 1 mm broad. Substance of lamina dense, sori sunken on lower surface but above forming ill-defined bulges. In basal web a vein anastomosing, other veins in sterile pinnules typically forking twice, branches reaching margin at 40° and at a concentration of 22 per cm, anastomosing only occasionally and then irregularly. In fertile parts of pinnules, lateral vein giving a forward branch to sorus and an outward branch which forks, branchlet nearest rachis almost perpendicular to margin. Indusium present, large but often lost and seldom visible without transfer. Sori at least 1 mm apart.

Matonidium goeppertii (Ettingshausen) Schenk, 1871. Pinnules usually less than 10 mm long and 2 mm wide, web along rachis narrow and with no anastomosing vein. Substance of lamina dense. Upper surface in sterile pinnule slightly convex, in fertile pinnule more convex and sori sometimes forming hemispherical bulges in contact with one another; bulges extending from midrib to margin. Veins once forked in most sterile pinnules, branches reaching margin at about 70° and at up to 50 per cm. In fertile pinnules veins forked, forward branch ending in a sorus, outward

branch sometimes forked again near margin and proximal branchlet perpendicular to margin (as in *M. braunii*), but successive sori at less than 1 mm apart.

In Yorkshire *M. goeppertii* is known from the Lower Deltaic only, where it is locally common, but elsewhere it occurs in younger rocks, particularly the Lower Cretaceous. Nearly all the Yorkshire leaves identified as *Matonidium goeppertii* in the BM (NH) agree fully with that species and form a homogeneous group including several excellent specimens. But a few fragments of *M. braunii* were determined as *M. goeppertii* and figured by Harris (1961) because they showed points of interest; they are from the Gristhorpe Bed (Middle Deltaic) and Saltwick (1961: figs 37A–C, E; figs 38A–G). There is now no detailed figure of the sorus of *M. goeppertii* from Yorkshire, nor has its spore been figured from anywhere except at a low magnification. The sori when exposed in transfer look just like the figures of *M. goeppertii* by Hirmer & Hoerhammer (1936), but as happens in *M. braunii* some of them have lost their sporangia and the indusium too, leaving merely a boss representing the placenta.

Phlebopteris polypodioides Brongniart, 1836. Pinnules commonly 40 mm × 5 mm, sometimes larger, basal web often 2 mm broad. Substance of lamina delicate and translucent. Sori not sunken and not projecting above. In basal web an anastomosing vein; veins otherwise essentially similar in sterile and fertile pinnules, laterals at once dividing into forward and backward branches which anastomose to form regular and somewhat rounded broad arches near midrib; sorus situated on primary arch. Branch veins arising from arch and reaching margin at an angle of about 60° and at a concentration of 20 per cm, occasionally branching further and anastomosing. Indusium probably absent.

The specimens now redetermined as *M. braunii* are a few collected from the Gristhorpe Bed in about 1830 and described under various names (see pp. 307–8). They were referred to *Phlebopteris polypodioides* by Seward (1900) and by Harris (1961) but did not fit well.

It should be noted that broad basal arches are not exclusive to *P. polypodioides*, for they occur also in *Piazopteris lorchi* Appert (1973) where the pinnules, though much shorter, have very similar venation.

Phlebopteris woodwardii Leckenby, 1864. (This species is almost always represented by fusainized (charred) pinnule fragments). Pinnules often 5 mm broad, sometimes broader; full length unknown but probably relatively long. Substance of lamina originally dense, preserved as uncompact charcoal showing individual cells. (Pinna rachis and basal web scarcely known). Veins (not known in basal web) forking and anastomosing to form primary arches which are higher than broad, branch veins arising from arch, forking and sometimes anastomosing, reaching margin at about 80° and a concentration of 50 per cm. Sorus situated in middle of primary vein arch, borne on a forward branch vein. Sorus strongly raised and forming a sharply bounded mound on upper surface, deeply sunken below. (Existence of indusium uncertain and details of sporangia poorly known).

The recognition of *Matonia braunii* in Yorkshire has made it necessary to reconsider the determination of certain unusual fragments determined as *P. woodwardii* which seemed to give additional information about the sorus. These fragments, from Roseberry Topping and from Hawsker, Jack Ass Trod are preserved as coaly compressions and showed *Matonidium*-like sporangia and a small indusium. I still think them rightly determined but the information they gave needs confirmation.

Apart from these compressed fragments, *P. woodwardii* is represented by widespread fusainized pinnule fragments, many of them fertile but all having entirely denuded placentae. They are occasionally abundant, along with fusainized wood. Hirmer & Hoerhammer (1936) removed the species from *Phlebopteris* and placed it in *Nathorstia* of the Marattiaceae, but I do not think that a sorus or synangium of this family would drop off from its placenta, even if scorched by fire. No other Yorkshire leaf is mainly known as fusain.

It is to be noted that this species and *P. dunkeri*, also included by Hirmer & Hoerhammer in *Nathorstia*, are known only as fragments, giving no evidence of the form of the whole leaf.

Distribution of *M. braunii*. Hirmer & Hoerhammer (1936) reduced a huge number of fossil species

to six and for two of them, *Phlebopteris braunii* and *P. muensteri*, they gave references to specimens spread over most of the northern hemisphere and ranging in age from the Trias to the Cretaceous. They wrote with such confidence that a reader may think the determination of a matoniaceous fossil from its figure is a clear-cut procedure to well-informed workers, as these two clearly were. But unfortunately it is not. As evidence for this I mention their treatment of the earliest named figure, Phillips' (1829) *Pecopteris caespitosa* (1936: 7). It heads their list for *Phlebopteris braunii* and also their list for *Matonidium goeppertii*, and as redrawn by Seward (1900) it is included in *Phlebopteris polypodioides*. This taxonomic slip arises from real difficulty and had they given *cf.* to each of these taxa, with cross references, I would have thought their treatment perfect.

Their long lists of citations under *P. braunii* and *P. muensteri* are valuable references to specimens of similar aspect. These specimens and later ones can be graded according to the published evidence. The most convincing is an assemblage of specimens showing matoniaceous leaf form with similar venation in sterile and fertile pinnules and no discordant feature. Just three regions produce such material: Bavaria (Franconia) and East Greenland, both in the lowest part of the Lias, and Yorkshire in the Bajocian. If we accept separate pinnae of suitable character we can add Bornholm, Middle or Upper Lias (Möller 1902), and Madagascar, Upper Jurassic (Appert 1973). If we omit the fertile venation (which is often very obscure) there is Poland, ?Upper Lias (Reymanówna 1963), and other localities in the Lower Lias of Bavaria (Kräusel 1958, Weber 1968). These specimens are excellent in other respects. Sikstel' (1960) figures similar pinnae under various names from central Asia (Upper Trias), but details are obscure in the published figures as are those from the Lias of Romania (Semaka 1956). Hirmer & Hoerhammer's citations of unfigured specimens form in my view a category without evidence.

Finally there are some figured specimens cited by Hirmer & Hoerhammer which fail to show the main diagnostic features and in my judgement also show a discrepant character. These include all specimens cited from the Cretaceous and from the Trias older than the Rhaetic, and also those from Asia and Africa.

Field key to the Yorkshire Matoniaceae

This key may fail with exceptional forms though normal forms are likely to occur with them.

- | | | |
|---|---|-----------------------------------|
| 1 | Specimens (pinnule fragments) preserved as fibrous fusain | <i>Phlebopteris woodwardii</i> |
| - | Specimens preserved as a continuous film of coal | 2 |
| 2 | Pinnules 10 mm × 2 mm or smaller | <i>Matonidium goeppertii</i> |
| - | Pinnules larger than 10 mm × 2 mm | 3 |
| 3 | Pinnules 5 mm or more broad | 4 |
| - | Pinnules less than 4 mm broad | 5 |
| 4 | Veins forming broad arches along midrib | <i>Phlebopteris polypodioides</i> |
| - | No arches along midrib, veins forming many small meshes | <i>Phlebopteris dunkeri</i> |
| 5 | Lamina thick; in sterile pinnule vein branches at a small angle; in fertile pinnule the branches nearly perpendicular | <i>Matonia braunii</i> |
| - | Lamina thin, basal vein arches present a small form of | <i>Phlebopteris polypodioides</i> |

Notes on fossil matoniaceous leaves described up to 1841

All the specimens cited below are from the Gristhorpe Bed apart from a few whose origin is mentioned.

1828 '*Polypodium*' Murray: 313; pl. 5, fig. 2. Fertile. Specimen not seen but figure looks like *P. polypodioides*.

1829 *Pecopteris caespitosa* Phillips: pl. 8, fig. 10. Specimen in Yorkshire Museum. No description and name therefore not valid. Refigured Phillips 1875: pl. 8, fig. 10 and with descriptive notes on p. 207

together with lign. 20, another specimen (from Haiburn). Original specimen redrawn by Seward (1900: fig. 8) as *Phlebopteris polypodioides*; this determination accepted by Harris (1961). Hirmer & Hoerhammer (1936) determined Phillips' drawing as *Phlebopteris braunii* and also as *Matonidium goeppertii* (1936: 18). Specimen in Phillips 1875: lign. 20 determined by Harris (1961) as *M. goeppertii*. Specimen of Phillips 1875: pl. 8, fig. 10 has its largest pinnules 17 mm × 3 mm, margins slightly depressed, web along pinna rachis narrow, substance of lamina thick and opaque, low bulges at 1 mm intervals perhaps representing denuded sori beneath; venation not observed (fine details damaged by varnish). Certainly not *Matonidium* but agrees well with *Matonia braunii*. I now think it unlikely to be *P. polypodioides* because substance is dense and pinnules are small. A few other Yorkshire Museum specimens determinable with confidence as *P. polypodioides* are labelled *P. caespitosa*.

1829 *Pecopteris crenifolia* Phillips: pl. 8, fig. 11. Drawing shows basal region of specimen in Yorkshire Museum. No description and name therefore not valid. Refigured by Phillips (1875), with description as *Phlebopteris crenifolia* and *P. propinqua* Lindley & Hutton included as a synonym. Specimen well preserved and normal *P. polypodioides*, pinnule margins mostly entire. The broad sori possibly give an illusion of lobing, but scarcely as in the figure. In places there are real bulges in the margin up to 0.5 mm high and these may be opposite sori or between them. At several points, however, the substance at the margins has flaked off or is overlapped by matrix and this gives some appearance of lobing. In the Yorkshire Museum there are also a few other specimens of *P. polypodioides* labelled *crenifolia* Phillips.

1832 or 1833 *Pecopteris polypodioides* Brongniart: pl. 83, fig. 1. Name on plate but description not published until 1836. Sterile pinna showing venation, specimen said to be in Paris.

1833 *Pecopteris polypodioides* Lindley & Hutton: 167; pl. 60 (*nomen nudum* of Brongniart 1828 misapplied). Specimen in Scarborough Museum but not seen by me; venation in figure agreeing with fertile *Matonia braunii*; accuracy of drawing confirmed by Phillips (1875: 202). Figure regarded by Seward (1900) and Harris (1961) as badly drawn *P. polypodioides*. Accepted as *P. braunii* by Hirmer & Hoerhammer (1936). Now accepted by me also as *M. braunii* because I know that leaves with venation as in the figure do occur in the Gristhorpe Bed. This confusing name has never come into use, see below.

1834 *Pecopteris propinqua* Lindley & Hutton: 101; pl. 119. A description and drawing by W. Williamson jr of a specimen collected by W. Williamson sr. Lindley & Hutton never saw the specimen and I have not recognized it in a museum. The figure strongly resembles that of *P. crenifolia* of Phillips, i.e. *P. polypodioides*. Williamson, though, compares it with *P. polypodioides* of Lindley & Hutton, i.e. *Matonia braunii*. The name *propinqua* never came into general use, see p. 309.

1835 *Phlebopteris contigua* Lindley & Hutton: 177; pl. 144. Specimen in good condition in Scarborough Museum. This is the first appearance in print of the genus *Phlebopteris* but it was not defined and therefore not valid. The text shows the authors had seen Brongniart's plate of *P. polypodioides* but supposed that their specimen, in fact typical *P. polypodioides*, was distinct. This name for *Phlebopteris polypodioides* never came into general use and although strictly valid I hope for this reason it will never be revived, see p. 309.

1836 *Phlebopteris* Brongniart: 371. Diagnosis and discussion of genus, first species described as *P. polypodioides*. Species now placed in *Dictyophyllum* were included in the genus.

1836 *Phlebopteris polypodioides* Brongniart: 372 (diagnosis, corresponding to figure, pl. 83, fig. 1, 1a already cited; see 1832 or 1833 above). Generally accepted as the holotype, though description is predated by the scarcely used and less well defined names *P. contigua* and *P. propinqua* of Lindley & Hutton.

1836 *Phlebopteris propinqua* Brongniart: 373; pl. 132, fig. 1; pl. 133, fig. 2. Same figures as *P. crenifolia* Phillips and *P. propinqua* Lindley & Hutton. *P. crenifolia* Phillips cited as synonym.

1836 *Phlebopteris schouwii* Brongniart: 374; pl. 132, figs 4, 4a, 5, 6. Sterile and fertile fragments from Lias of Bornholm. Specimens considered by Möller (1902: pl. 46) as possibly *P. woodwardii* but otherwise indeterminate; accepted by some authors as *P. polypodioides*.

1836 *Polypodites crenifolius* Goepfert: 343, for *Pecopteris crenifolia* Phillips and *Pecopteris propinqua* Lindley & Hutton.

1836 *Polypodites lindleyi* Goepfert: 342; pl. 38, figs 1, 2, for *Pecopteris polypodioides* Lindley & Hutton. Name *lindleyi* applied to a few specimens of *P. polypodioides* in the Yorkshire Museum, but later dropped.

1838 *Laccopteris elegans* Sternberg: 115; pl. 32, figs 1-3, 8a-c. A block showing sterile and fertile pinnule fragments from the Lower Lias of Bavaria. Specimen re-examined by Jung & Knobloch (1972) who remained uncertain about its nature; see p. 309.

1841 *Laccopteris braunii* Goepfert, Lief 1-2 (2): 7; pl. 5, figs 1-7. Lower Lias, Bavaria. The specimen in fig. 1 is considered here to be the Type.

1841 *Laccopteris germinans* Goepfert, Lief 1-2 (2): 9; pl. 6, figs 1-12. Lower Lias, Bavaria. (Widely regarded as leaves of young plants of *L. braunii*).

Summary

This work leaves the validity of three important specific names uncertain.

Is *Laccopteris braunii* Goepfert, 1841 identical with *Laccopteris elegans* Sternberg, 1838? Many have thought so, for example Hirmer (1927), but later he changed his mind and with Hoerhammer (1936) firmly separated *Laccopteris elegans* as a marattiaceous fern with round sori. The matter can only be settled by a fresh study of Bavarian material. If for example specimens matching the original figures were discovered which have unmistakable synangia I would be convinced. At present I am not but leave the name *braunii* standing.

There are still earlier descriptions of *braunii* under other names. Of these, Phillips' (1829) *Pecopteris caespitosa* (see p. 307) is not valid because there is no description. The name *Pecopteris polypodioides* of Lindley & Hutton, 1833, raises a difficult problem. The matter is complicated by the almost simultaneous publication of the relevant works of Brongniart (1828–36) and Lindley & Hutton (1831–37) in numerous parts. Both include descriptions of plants from the Gristhorpe Bed. Another complication is caused by Brongniart's publication of many *nomina nuda* and also of named figures without descriptions, both being completed in later parts. Lindley & Hutton deeply respected Brongniart and co-operated with him and treated his *nomina nuda* as valid names, even when unsure how they applied.

The first matoniaceous fern of Brongniart, 1828, is his *nomen nudum* *Pecopteris polypodioides*. The first description in valid form is of a fertile pinna showing the specific character of *braunii* by Lindley & Hutton (1833: pl. 60). The description is good but unfortunately they misapplied Brongniart's *nomen nudum* to their specimen. The words '*Pecopteris polypodioides* Brongniart p. 57'. In the text they say: 'It is evident that our fossil is referable to Adolphe Brongniart's genus *Pecopteris*; but as the figures illustrative of that genus are not yet published, we have no means of knowing to what species; we conjecture only that it must be his *P. polypodioides*, from the aptness of the name, and from its having been procured by him from the Lower Oolite'. Soon after they wrote this, Brongniart's (1832 or 1833) named figure of *P. polypodioides* was published and their error was plain. They had a new species. Can we accept Lindley & Hutton's expressed doubt as making the application of the name *polypodioides* to their specimen infirm and therefore not valid in nomenclature? It would be greatly in the interests of palaeobotany to do so and this is the view I take. So *polypodioides* L. & H. is not after all the first valid name of *braunii*. But some may disagree.

I turn to *P. polypodioides* of Brongniart. Its earliest named figure, *Pecopteris crenulata* Phillips, 1829, has no description. After Lindley & Hutton had seen Brongniart's (1832 or 1833) figure they received Williamson's drawing which they published (1834: pl. 119) under the name *Pecopteris propinqua*. They recognized that the veins were as in *P. polypodioides* of Brongniart, but considered that the lobed margins of the pinnules distinguished it. I suppose that the specimen is like Phillips' drawing of *P. crenulata*, a fertile pinna where the figure gives an exaggerated impression of lobes and that it is merely a somewhat inaccurate drawing of *polypodioides* Brongniart, but as I have not seen the specimen I cannot be as sure as I am about Phillips' very similar figure. The next validly published name is *Pecopteris contigua* Lindley & Hutton, 1835: pl. 144. The figure and the specimen itself show the venation of a typical specimen of *P. polypodioides* but Lindley & Hutton thought that its crowded pinnules distinguished it. All later authors have considered it well within the form range of *P. polypodioides* and have dropped the name *contigua*, though I can see no way in which this can be done in accordance with the Code.

Thus as I see it, the name *braunii* (or *elegans*) is saved, though by a narrow margin, from becoming '*polypodioides* L. & H.'. But the valid name for Brongniart's species is either *propinqua* L. & H. or *contigua* L. & H.

I have never flouted the Botanical Code but may have breached it inadvertently. But now I continue to use the name *polypodioides*. To change it wastes time and causes frustration. Palaeobotanists will be aware that there is nothing basic in taxonomy that makes this change of name necessary. There are only the provisions of the Code and rulings of Botanical Congresses against the conservation of any specific name, though they did agree to conserve generic names. Had these fossils been animals there would have been little difficulty. The zoologists (including palae-

ontologists) can and do conserve old specific names. They could have surmounted the trouble caused by *polypodioides* L. & H. in that way, but I suppose they could, as an alternative, have deemed that Brongniart's drawing was published slightly earlier (as it may have been) and accepted it as a valid characterization of the species, cutting out the Lindley & Hutton figure and name and making *propinqua* and *contigua* synonyms.

I state the facts as I see them and leave the name *Phlebopteris polypodioides* standing and merely express the hope that before anyone changes it, the Botanical Code will be altered in a way which will make this name regular.

These nomenclatorial difficulties began through ordinary taxonomic errors. I think they were at first perpetuated through the early palaeobotanists having in their minds principles other than that of priority of publication, or at least they did not give that overwhelming weight. To some, admiration for Brongniart's masterly work was a reason for preferring his names to ones published a year or two earlier. Much later, Seward in his revisions of Mesozoic floras was unwilling to put nomenclatorial priority over the advantages of letting a well-understood name continue to stand; that is on his own judgement he conserved specific names. These names still stand.

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References

- Appert, O. 1973. Die Pteridophyten aus dem Oberen Jura des Manamana in Südwest-Madagaskar. *Schweiz. paläont. Abh.*, Basel, **94** : 1-62, 90 pls.
- Brongniart, A. 1828. *Prodrôme d'une Histoire des Végétaux fossiles*. viii + 223 pp. Paris.
- 1828-38. *Histoire des végétaux fossiles, ou recherches botaniques et géologiques sur les végétaux renfermés dans les divers couches du globe*. **1**. xii + 488 pp, 171 pls. Paris. Parts cited (dates taken from Zeiller 1903: 306) Liv. 7: 265-288, pls 83-97, 1832 or 1833; Liv. 11: 369-416, pls 135-146, 1836.
- Goepfert, H. R. 1836. Die fossilen Farrnkräute (Systema filicum fossilium). *Nova Acta physico-med.*, Halle a.S., **17** (Suppl.). xxxiii + 488 pp., 44 pls.
- 1841-46. *Die Gattungen der fossilen Pflanzen verglichen mit denen der Jetztwelt und durch Abbildungen erläutert*. 151 pp., 51 pls. Bonn.
- Harris, T. M. 1926. The Rhaetic Flora of Scoresby Sound, East Greenland. *Meddr Grønland*, Copenhagen, **68** : 45-148, pls 1-13.
- 1931. The Fossil Flora of Scoresby Sound, East Greenland. 1. Cryptogams (exclusive of Lycopodiales). *Meddr Grønland*, Copenhagen, **85** (11) : 1-102, pls 1-18.
- 1961. *The Yorkshire Jurassic Flora*, **1**. *Thallophyta-Pteridophyta*. ix + 212 pp. London, Brit. Mus. (Nat. Hist.).
- Hirmer, M. 1927. *Handbuch der Paläobotanik*. xvi + 708 pp., 817 figs. Munich & Berlin.
- & Hoerhammer, L. 1936. Morphologie, Systematik und geographische Verbreitungen der fossilen und rezenten Matoniaceen. *Palaeontographica*, Stuttgart, **B 81** : 1-70, pls 1-10.
- Jung, W. & Knobloch, E. 1972. Die 'STERNBERG-Originale' der Bayerischen Staatssammlung für Paläontologie und historische Geologie zu München. *Mitt. bayer. St. Paläont. Hist. Geol.*, Munich, **12** : 105-111.
- Kräusel, R. 1958. Die Juraflora von Sassendorf bei Bamberg. *Senckenberg. leth.*, Frankfurt a.M., **39**, 1-2: 67-102, pls 3-8.
- Leckenby, J. 1864. On the sandstones and shales of the Oolites of Scarborough, with descriptions of some new species of fossil plants. *Q. Jl geol. Soc. Lond.* **20** : 74-82, pls 8-11.
- Lindley, J. & Hutton, W. 1831-37. *The fossil flora of Great Britain; or, figures and descriptions of the vegetable remains found in a fossil state in this country*. **1** (1831-33), li + 223 pp., pls 1-79. **2** (1833-35), xxvii + 208 pp., pls 80-156. **3** (1835-37), 208 pp., pls 157-230. London.

- Lundblad, A. B. 1950. Studies in the Rhaeto-Liassic floras of Sweden. 1. Pteridophyta, Pteridospermae and Cycadophyta from the mining district of N.W. Scania. *K. svenska Vetensk Akad. Handl.*, Stockholm, (4) 8 : 1-82, pls 1-13.
- Möller, H. 1902. Bidrag till Bornholms fossila flora. Pteridofyter. *Acta Univ. lund.* 38 2 (5) : 1-63, pls 1-6.
- Murray, P. 1828. Account of a Deposit of Fossil Plants, discovered in the Coal Formation of the Third Secondary Limestone, near Scarborough. *Edinb. new phil. J.* 5 : 311-317, pl. 5.
- Phillips, J. 1829. *Illustrations of the Geology of Yorkshire, or a description of the strata and organic remains of the Yorkshire coast* (i.e. Part 1, 1st edn). xvi + 192 pp., 9 + 14 pls. York.
- 1875. *Illustrations of the Geology of Yorkshire; or, a description of the strata and organic remains. Part I, The Yorkshire Coast.* (3rd edn, ed. Etheridge, R.) xii + 354 pp., 28 pls, map. London.
- Reymanówna, M. 1963. 1. Review of investigations on Polish Jurassic floras. 2. The Jurassic flora from Grojec near Cracow in Poland, Part I. *Acta palaeobot. Cracov.* 4 (2) : 1-48, pls 1-9.
- Schenk, A. 1865-67. *Die fossile Flora der Grenzschichten des Keupers und Lias Frankens.* xxiv + 232 pp., Atlas 45 pls. Wiesbaden.
- 1871. Beiträge zur Flora der Vorwelt, IV. Die Flora der nordwestdeutschen Wealdenformation. *Palaeontographica*, Stuttgart, 19 : 203-262, pls 22-43.
- Semaka, A. 1956. Contribuții la Flora Liasică de la Vulcan-Codlea. Nota II. *Buletin sti. Acad. Republ. pop. Rom.* (ser. Geol. Geogr.), Bucharest, 1 (1-2) : 107-121, figs 1-30.
- Seward, A. C. 1899. On the structure and affinities of *Matonia pectinata* R. Br. with notes on the geological history of the Matonineae. *Phil. Trans. R. Soc.*, London, B 191 : 171-209, pls 17-20.
- 1900. The Jurassic Flora. I, The Yorkshire Coast. *Catalogue of the Mesozoic Plants in the Department of Geology, British Museum (Natural History)*. 3, xii + 341 pp., 21 pls. London.
- Sikstel', T. A. 1960. [Stratigraphy of the continental deposits of the upper Permian and Triassic of Central Asia.] *Trudy tashkent. gosud. Univ.* (n.s.) 176 : 1-147, pls 1-19 (numbered as pages). [In Russian].
- Sternberg, C. von 1820-38. *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt.* 200 pp., 70 pls col. Leipzig & Prague.
- Walton, J. 1936. On the factors which influence the external form of fossil plants; with descriptions of the foliage of some species of the Palaeozoic Equisetalean genus *Annularia* Sternberg. *Phil. Trans. R. Soc.*, London, B 226 : 219-237, pls 31, 32.
- Weber, R. 1968. Die fossile Flora der Rhät-Lias-Übergangsschichten von Bayreuth (Oberfranken) unter besonderer Berücksichtigung der Coenologie. *Erlanger geol. Abh.* 72 : 1-73, pls 1-17.
- Zeiller, R. 1903. Flore fossile des Gîtes de Charbon du Tonkin. viii + 328 pp., 56 pls. *Étud. Gîtes minér. Fr.*, Paris.